

HUMAN MUSCLE STRENGTH TRAINING: THE EFFECTS OF THREE DIFFERENT REGIMES AND THE NATURE OF THE RESULTANT CHANGES

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SUMMARY

1. Increases in strength and size of the quadriceps muscle have been compared during 12 weeks of either isometric or dynamic strength training.

2. Isometric training of one leg resulted in a significant increase in force ($35 \pm 19\%$, mean \pm S.D., $n = 6$) with no change in the contralateral untrained control leg.

3. Quadriceps cross-sectional area was measured from mid-thigh X-ray computerized tomography (c.t.) scans before and after training. The increase in area ($5 \pm 4.6\%$, mean \pm S.D., $n = 6$) was smaller than, and not correlated with, the increase in strength.

4. The possibility that the stimulus for gain in strength is the high force developed in the muscle was examined by comparing two training regimes, one where the muscle shortened (concentric) and the other where the muscle was stretched (eccentric) during the training exercise. Forces generated during eccentric training were 45% higher than during concentric training.

5. Similar changes in strength and muscle cross-sectional area were found after the two forms of exercise. Eccentric exercise increased isometric force by $11 \pm 3.6\%$ (mean \pm S.D., $n = 6$), and concentric training by $15 \pm 8.0\%$ (mean \pm S.D., $n = 6$). In both cases there was an approximate 5% increase in cross-sectional area.

6. It is concluded that as a result of strength training the main change in the first 12 weeks is an increase in the force generated per unit cross-sectional area of muscle. The stimulus for this is unknown but comparison of the effects of eccentric and concentric training suggest it is unlikely to be solely mechanical stress or metabolic fluxes in the muscle.

INTRODUCTION

Increased strength and skeletal muscle hypertrophy are well-known consequences of functional overload (Goldberg, Etlinger, Goldspink & Jablecki, 1975; McDonagh & Davies, 1984) and yet there remain several areas of fundamental ignorance. There are, for instance, doubts as to whether the increase in strength can be adequately explained by the increase in size of the muscle and although it is generally agreed that changes are induced by high-intensity exercise it is not clear what aspect of this activity, such as mechanical stress or increased metabolic flux, is the stimulus for growth.

The major determinant of skeletal muscle strength is the cross-sectional area of the contractile material and linear relationships between size and strength have been demonstrated in the human quadriceps (Young, Stokes, Round & Edwards, 1983; Chapman, Edwards, Grindrod & Jones, 1984). However, within any group of subjects there can be considerable variation, probably due to a number of factors including differences in the lever system through which the muscle acts, the angle of pennation of the fibres or the fibre-type composition (Alexander & Vernon, 1975; McCullough, Maughan, Watson & Weir, 1984; Young, 1984). There have been few studies comparing changes in muscle force and size with training, but where accurate measurements of area have been made together with assessments of strength that are not confused with learning effects, the surprising conclusion has been that the increase in muscle strength was greater than could be explained by the increase in muscle size alone (Ikai & Fukunaga, 1970; Young *et al.* 1983).

The critical stimulus for an increase in strength provided by high levels of activity is as yet unknown, although the consensus of opinion favours high mechanical stress (Goldberg *et al.* 1975). Another consequence of this type of contraction will be large metabolic fluxes (mainly glycolytic) the products of which could also act as a stimulus for adaptation to high work loads. During eccentric (lengthening) contractions high forces are generated by the muscle at a relatively low metabolic cost compared with either isometric or concentric (shortening) contractions (Katz, 1939; Abbott, Bigland & Ritchie, 1952; Curtin & Davies, 1973). A comparison of the changes resulting from eccentric and concentric contractions should therefore distinguish between the two possible stimuli, i.e. mechanical stress and metabolic cost. Several studies have compared the strengthening effects of these two types of contraction (for review see Rasch, 1974) but in only one have eccentric contractions been shown to cause greater increases in strength (Komi & Buskirk, 1972). A feature of many of these studies has been the use of the same absolute weight for both concentric and eccentric training so that the mechanical stress was the same (Logan, 1952; Seliger, Dolejas, Karas & Pachlopnikova, 1968; Johnson, 1972). In these circumstances the difference between the two forms of exercise would be the metabolic cost and the findings therefore suggest that metabolic cost is not the critical stimulus. The complementary experiment would be to use heavier training weights during eccentric exercise so that the mechanical stress is greater for the same or smaller metabolic cost.

In the work described here we have examined the effects of weight-training regimes on muscle strength, size, muscle activation and radiological density. We have also compared the effects of eccentric and concentric exercise, using appreciably higher loads for the eccentric training to assess the value of mechanical stress as a stimulus for improvements in strength.

METHODS

Subjects. Twelve healthy adult subjects (eleven male, one female) took part in this study. None had previously taken part in regular weight training. Six subjects performed unilateral isometric training with the contralateral leg acting as a control. The other six subjects trained one leg with concentric contractions and the other leg with eccentric contractions. All subjects gave their full informed consent and the study was approved by the Committee for the Ethics of Human Procedures, University College Hospital. The physical characteristics of the subjects are given in Table 1.

Training. The study comprised three separate training regimes for the quadriceps muscle with six legs in each. In each study subjects trained three times a week for 12 weeks. Each session consisted of four sets of six repetitions with a 1 min rest period between each set.

Isometric training. Six subjects trained using unilateral isometric contractions performed in the strength-testing chair as described below. The contralateral leg was not trained and acted as a control. The training was randomized between the dominant and non-dominant leg. At the

TABLE 1. Physical characteristics of subjects

Training study	Age (years)		Height (cm)		Weight (kg)	
	Mean	S.D.	Mean	S.D.	Mean	S.D.
Concentric and eccentric	27.5	6.3	172.1	11.1	69.0	4.0
Isometric	27.5	5.7	171.5	6.4	64.5	7.3

beginning of each week the maximum isometric force of the quadriceps was tested and a visual training target set to 80% of maximum. Each contraction was held for 4 s with a 2 s rest between each. One of the subjects trained for only 8 weeks.

Concentric and eccentric training. Six subjects (five male, one female) trained one leg with concentric and the other leg with eccentric contractions. Training was carried out on an Atlanta variable-resistance leg-extension machine (Rotherham, U.K.) moving through a knee angle from 45 to 180 deg. Subjects trained at a weight that could just be lifted or lowered six times, which was about 80% of the weight that could just be lifted once. The weights were either lifted or lowered by a helper for the two types of contraction. The weights lowered during the eccentric exercise were on average 145% of those lifted during the concentric training. The six repetitions in each set were carried out within 30 s, the contraction lasting 2–3 s with a similar rest period between. The eccentric and concentric training was randomized between dominant and non-dominant legs.

Measurement of strength. Maximum isometric voluntary contraction force (m.v.c.) of the quadriceps was measured as described by Edwards, Young, Hosking & Jones (1977). The best of three m.v.c.s was measured before, every 2 weeks during and at the end of training. A percutaneous twitch superimposition technique was used to assess whether subjects were able to maximally activate the quadriceps during an m.v.c. The quadriceps was stimulated at 1 Hz with a voltage sufficient to activate over 50% of the muscle and the height of the twitches before and during a voluntary contraction were compared. During a truly maximum contraction no extra force is generated by the stimulation, but when the contraction is submaximal the height of the superimposed twitch can be used to estimate the degree of inhibition (Rutherford, Jones & Newham, 1986). For subject W. K. (Fig. 2) the superimposed twitches were approximately 20% of the twitches before the voluntary effort indicating that the voluntary contraction was 20% less than the true maximum.

Measurement of quadriceps size. Quadriceps cross-sectional area was measured from computerized tomography (c.t.) scans taken before and after the 12 weeks of training. Subjects were scanned midway between the greater trochanter and tibial femoral joint space in the supine position with the muscles relaxed. All scans were performed on a Philips Tomoscan 310 with a scanning time of 4.8 s and a slice thickness of 9 mm.

To ensure that repeat scans were taken at the same position, a map was constructed on a plastic sheet showing the c.t. scan site in relation to blemishes and moles on the thigh. Where there were no suitable marks on the leg, the height from the floor to the scan site was measured using a Holstan anthropometer.

The c.t. images were analysed off-line on a locally designed interactive system (Grindrod, Tofts & Edwards, 1983) to give measurements of quadriceps cross-sectional area and mean Hounsfield number (unit of radiological density; Bulcke, Termote, Palmers & Crolla, 1979). Quadriceps area was measured semi-automatically with a contour-following programme and manual editing (Fig. 1). Estimates of muscle density were made by measuring the mean Hounsfield number from three discrete sites in the quadriceps. A scanning artifact is present across the centre of the image which gives rise to spurious density readings so the sampling areas were selected from sections of the

image unaffected by this artifact. The coefficient of variation of seven repeated measurements of mean Hounsfield number on two subjects was less than 5%.

Electromyogram (e.m.g.) activity. Measurements of integrated e.m.g. were made during each type of contraction. The skin surface was prepared by rubbing the skin with emery paper and washing with alcohol. Recordings were made from vastus lateralis using Medelec EA 1000 surface electrodes with pre-amplifiers and the amplified signal was integrated at 10 Hz. A potentiometric goniometer was attached to the leg with the centre of rotation at the knee. The signal was displayed together with the integrated e.m.g. so that the extent of activation during different parts of the movement could be assessed.

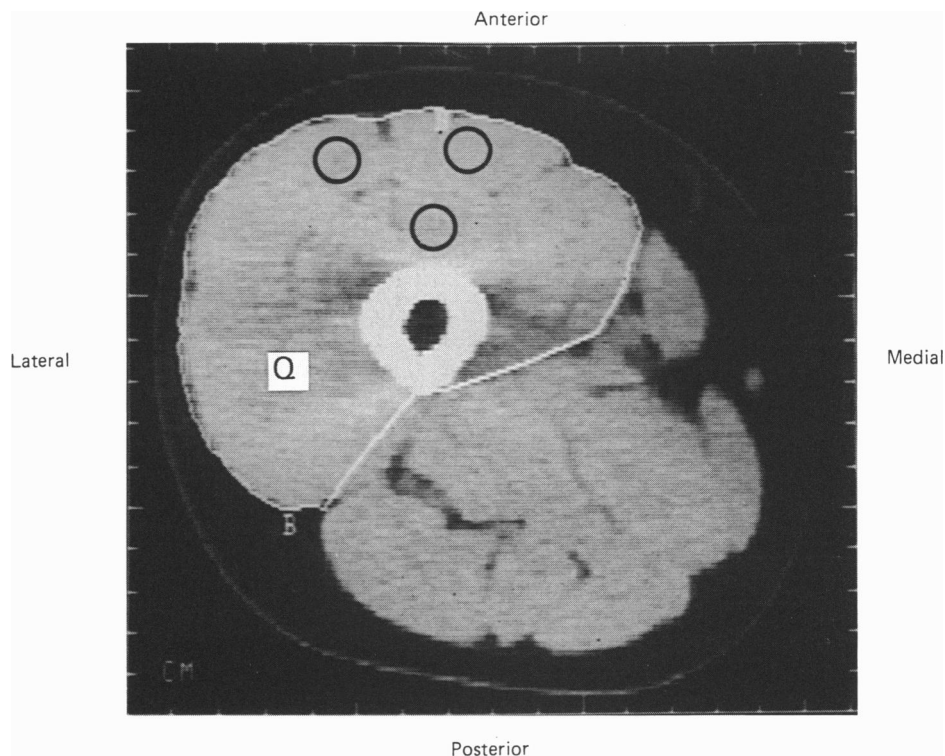


Fig. 1. A c.t. scan image taken at mid-thigh from a male subject with the quadriceps (Q) and areas sampled for density outlined.

RESULTS

Isometric training

Subjects had no difficulty performing the training exercises. Two subjects experienced appreciable pain and stiffness in the first week but this disappeared by the second week. Only one subject was found not to be able to fully activate the quadriceps before the training began. Records of voluntary contractions from this subject before and after training are shown in Fig. 2 and are compared with another subject who was able to achieve full activation. At the end of the training programme all subjects were able to fully activate their muscles. Where there was evidence of incomplete activation the true maximum force has been estimated from the size of the superimposed twitch.

The c.t. scans were carried out before and at the end of the training programmes.

A scan from a male thigh is shown in Fig. 1 indicating the area of the quadriceps measured and the regions sampled for density measurements.

Absolute values for force, quadriceps area and density are given in Table 2, and the percentage changes are shown in Fig. 3. There was a large and significant increase in isometric force after the isometric training ranging from 18–65% ($35 \pm 19\%$, mean

TABLE 2. Quadriceps strength (m.v.c.), cross-sectional area and radiological density before and after training. Results given as mean (\pm s.d.)

Study	m.v.c. (N)		Cross-sectional area (cm ²)		Hounsfield number	
	Pre-training	Post-training	Pre-training	Post-training	Pre-training	Post-training
Concentric	521 (122)	601 (146)	66.3 (8.9)	70.1 (9.6)	61.6 (5.0)	63.8 (3.7)
Eccentric	516 (122)	572 (144)	68.7 (12.4)	71.1 (11.9)	60.1 (5.1)	63.3 (5.0)
Isometric	591 (112)	793 (159)	76.9 (15.5)	80.6 (14.2)	62.6 (5.8)	66.3 (6.0)
Control	619 (87)	662 (138)	73.8 (10.7)	74.3 (12.0)	65.0 (3.1)	66.0 (2.8)

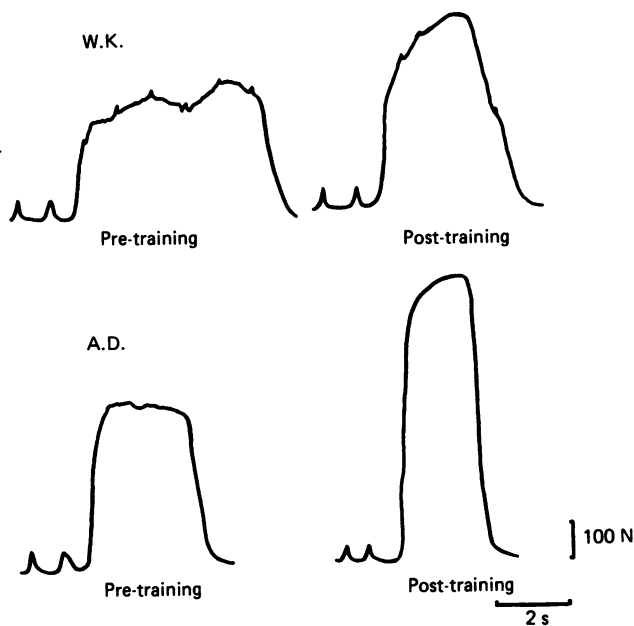


Fig. 2. Tracings of m.v.c. with superimposed electrical stimulation before and after training in two subjects. Subject W.K. had 20% inhibition prior to training and increased in maximum strength by 18%. Subject A.D. had no inhibition prior to training and increased in strength by 65%.

\pm s.d., $P < 0.01$, paired measurements). There was no significant difference in the strength of the control leg; after 12 weeks the strength increased by $6 \pm 8\%$ (mean \pm s.d., $P > 0.2$, paired measurements).

There was a small but significant increase in the cross-sectional area of the trained quadriceps muscle (Table 2, range 0–11%, $5 \pm 4.6\%$, mean \pm s.d., $P < 0.05$, paired measurements). This, however, was smaller than the increase in force and there was no suggestion of a correlation between changes in force and cross-sectional area. The greatest increase in force was 65% with a 3.3% increase in area, whilst an 11% increase in cross-sectional area was associated with only an 18% increase in force.

As a consequence of these changes the force per unit area of the trained quadriceps increased significantly from 7.7 ± 0.7 to 9.8 ± 1.0 N/cm² (mean \pm s.d., $P < 0.01$, unpaired t test). There was no significant change in this ratio for the control leg, changing from 8.5 ± 1.1 to 8.9 ± 1.1 (mean \pm s.d., $P > 0.5$) over the 12 week period. The coefficient of variation for the measurement of force per unit area estimated from the duplicate measurements made 12 weeks apart on the control leg was 6.5%.

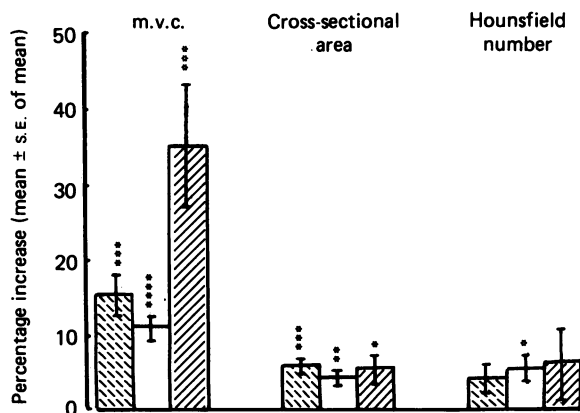


Fig. 3. Percentage increase in quadriceps isometric force, cross-sectional area and Hounsfield number after 12 weeks of either concentric (dashed hatching), eccentric (open), or isometric (hatched) training. (Significance from pre-training values, Student's paired t test. * $P < 0.05$, ** $P < 0.02$, *** $P < 0.01$, **** $P < 0.001$.)

There was a small increase in the radiological density of the quadriceps as a result of training (Table 2). No change was seen in the control leg.

Comparison of eccentric and concentric training

No difficulty was experienced by any of the subjects with the exercise and all were able to fully activate their quadriceps muscles during the isometric contractions used to monitor their progress.

The weights supported by the leg carrying out the eccentric training were on average 145% of the weights supported by the leg trained with concentric contractions. After 12 weeks the training weights were 261 and 250% of the initial values respectively for the eccentric and concentric legs. The increase in training weights was similar to that seen in a previous study of dynamic weight training (Rutherford & Jones, 1986). Despite this large improvement, isometric strength showed a more modest change increasing by $11 \pm 3.6\%$ (mean \pm s.d.) for the eccentric legs and $15 \pm 8.0\%$ for the concentrically trained legs. There was no statistically significant difference between the strength gains as a result of the two forms of exercise ($P < 0.1$, unpaired t test). The increase in strength was significantly less ($P < 0.05$, unpaired t test) than found as a result of the isometric training.

There were increases in muscle cross-sectional area after both training regimes (4–6%, Table 2, Fig. 3), but with no significant differences between either the two forms of dynamic training or the isometric training ($P > 0.1$, unpaired t tests). As with the isometric training there was no suggestion of a correlation between change in strength and change in quadriceps area.

There were small increases in radiological density as a result of the two forms of training (Table 2, Fig. 3) and this was also similar to that seen after isometric training.

Electrical activity during the different training exercises

The total integrated e.m.g. activity for isometric contractions was about twice that for either the eccentric or concentric contractions. A typical set of integrated e.m.g. and goniometer records are shown in Fig. 4. It can be seen that activation

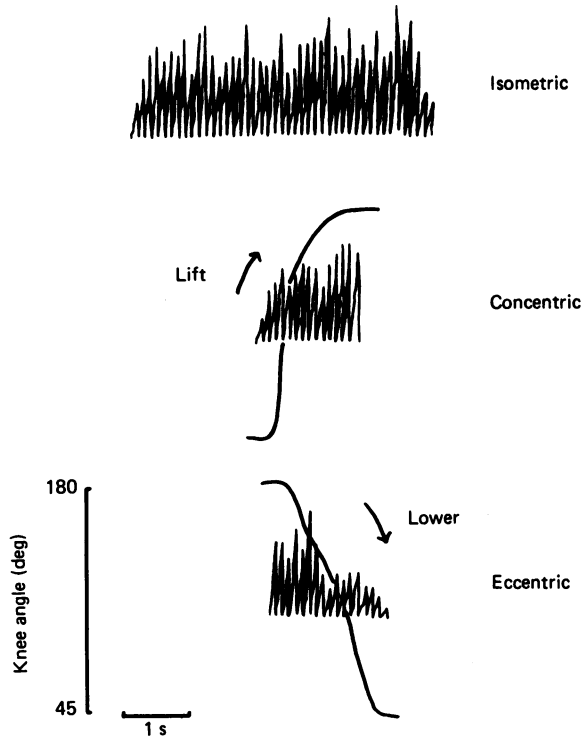


Fig. 4. Tracings of integrated e.m.g. records made during three types of training contraction. Goniometer readings are superimposed during dynamic contractions.

was only high during the hold (or isometric) phases of the dynamic movements. During the isometric contraction, activation was high and relatively constant throughout the contraction which also lasted for a longer time.

These observations suggest that the larger increase in force seen as a result of the isometric training may be explained by the greater degree and duration of muscle activation when compared to the dynamic training.

DISCUSSION

Changes in strength and size with training

Substantial increases in quadriceps force were observed as the result of all forms of training. After 12 weeks of isometric training there was an increase of around 35% which was similar to changes reported by a number of workers (e.g. Lindh, 1979). The

increase in isometric force was greater than the increase in muscle cross-sectional area (around 5%) so that the force per unit area increased by about 25% as a result of the training. Dynamic training had a similar effect; although the strength gain was less than with the isometric exercise it was still greater than the change in muscle area. The measurements of maximum voluntary force and quadriceps area from c.t. scans can both be subject to a variety of errors. However, the fact that similar changes were seen after three different training programmes and the low coefficient of variation for repeat measurements of the control limb suggest that the observed increase in force per unit area was not artifactual. Our findings therefore agree with those of Ikai & Fukunaga (1970) and Young *et al.* (1983) who also found an increase in strength which was greater than could be accounted for by a change in the cross-sectional area of the muscle.

The most commonly proposed explanation for this disparity is that the improvement in force is due either to a learning effect or increased activation of the muscle as a result of changes in the motor unit firing patterns (Moritani & DeVries, 1979; Häkkinen & Komi, 1985). With isometric contractions of the quadriceps, however, learning effects are minimal. The subjects are securely seated with a lap strap and back support so other muscle groups are not involved in the generation of force, and it can be seen from the data for the control leg (see Table 2) that there was no learning over a 12 week period. We have evidence in these studies from superimposed stimulation that, with one exception (W.K.), all subjects were able to fully activate their quadriceps muscles both before, during and after the training.

There is some evidence from both human and animal work that type II fibres are intrinsically stronger than type I (Bárány & Close, 1971; Young, 1984) so that preferential hypertrophy of type II fibres could lead to an increase in the force per unit area of mixed muscle. Although preferential hypertrophy of type II fibres has been shown in elite power athletes (Tesch & Larsson, 1982; MacDougall, Sale, Elder & Sutton, 1982) the evidence for this occurring in short-term training studies is contradictory (MacDougall, Elder, Sale, Moroz & Sutton, 1980; Young *et al.* 1983). Where selective hypertrophy has been found, the differences have been too small to account for the disparity between changes in strength and size (Thorstensson, Hultén, von Döbeln & Karlsson, 1976; MacDougall *et al.* 1980).

Fibres in the quadriceps muscle do not lie parallel to the line of action of the muscle, rather they insert into the tendons at acute angles. A change in this angle of insertion (or pennation) may alter the force measured between the ends of the muscle. For the same length and cross-section of muscle an increased angle of pennation can result in more contractile material being attached to a larger area of tendon (Alexander & Vernon, 1975). If, therefore, as a result of training, larger fibres attach to the tendon at a greater angle, then, with some readjustment in fibre length, the increase in strength could be greater than the over-all increase in anatomical cross-sectional area.

A consistent finding in all three of the training regimes studied, and in the study of Horber, Scheidegger, Grünig & Frey (1985), was that the radiological density of the muscle showed a small but consistent increase. This could occur for a number of reasons: a decrease in the fat content of the muscle, an increase in the packing of the contractile elements or an increase in the connective tissue content. A consequence of the former two possibilities would be an increase in the force per unit area.

It is generally assumed that tension is transmitted longitudinally in a muscle fibre through serial sarcomeres so that the force is proportional only to the cross-sectional area and independent of the length. If, however, attachments are made between the tendons and intermediate sarcomeres this would increase the force generated per unit cross-sectional area of the muscle. Mammalian muscle fibres are enveloped in a connective-tissue matrix which could play some role in transmitting tension to the tendons and work-induced hypertrophy is known to increase collagen synthesis in animal muscle (Schiaffino, Bornioli & Aloisi, 1972; Goldberg *et al.* 1975).

If connective tissue attachments were made at intermediate points of the fibres their effective length and therefore velocity of shortening, would be decreased. As power output is determined by both the force and velocity of contraction, a greater increase in force than power output will be a consequence of these attachments. Preliminary data on the effect of strength training on the power output of the quadriceps supports this hypothesis (Rutherford, Greig, Sargeant & Jones, 1986).

The stimulus for increase in strength

The comparison of eccentric and concentric training showed neither to be more effective than the other in increasing strength. During eccentric training the weights used were approximately 50% greater than for the concentric training but otherwise the training protocols were the same. The metabolic cost of eccentric contractions is smaller than for concentric contractions generating the same work. Bigland-Ritchie & Woods (1976) estimated the metabolic cost of concentric work to be nearly six times that of eccentric work and, whilst others have arrived at lower values, it is clear that the difference is considerable. If, therefore, the stimulus for an increase in strength were high mechanical stress or metabolic cost, one or the other of the two forms of training should have proved more effective. That this was not the case strongly suggests that neither of these factors alone is the single stimulus for adaptation in the muscle. The stimulus may either be related to the various processes of activation or some combination of mechanical stress and metabolic cost. A third possibility is that there is a threshold level of mechanical stress for adaptation which was achieved in both studies.

We have demonstrated increases in strength which are not attributable to muscle hypertrophy; nevertheless it is common experience that dedicated weight lifters and power athletes do undergo considerable muscular development. These people have usually trained more intensively and for longer periods of time than our subjects. We suggest, therefore, that there may be two responses to heavy exercise. The first is an increase in strength without an increase in over-all size due, possibly, to changes in fibre size and attachment to tendons or proliferation of connective tissue which can transmit force from intermediate points of the fibre to the tendons. This may occur fairly rapidly in the first 6–12 weeks of training. The second stage may be a slower process of gross muscular hypertrophy. Because of the difficulties of organizing controlled trials most studies, including our own, have been concerned only with the first of these types of adaptation.

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REFERENCES

- ABBOTT, B. C., BIGLAND, B. & RITCHIE, J. M. (1952). The physiological cost of negative work. *Journal of Physiology* **117**, 380–390.
- ALEXANDER, R. MCN. & VERNON, A. (1975). The dimensions of the knee and ankle muscles and the forces they exert. *Journal of Human Movement Studies* **1**, 115–123.
- BÁRÁNY, M. & CLOSE, R. I. (1971). The transformation of myosin in cross-innervated rat muscles. *Journal of Physiology* **213**, 455–474.
- BIGLAND-RITCHIE, B. & WOODS, J. J. (1976). Integrated electromyogram and oxygen uptake during positive and negative work. *Journal of Physiology* **260**, 267–277.
- BULCKE, J. A., TERMOTE, J. L., PALMERS, Y. & CROLLA, D. (1979). Computed tomography of the human skeletal muscular system. *Neuroradiology* **17**, 127–136.
- CHAPMAN, S. J., EDWARDS, R. H. T., GRINDROD, S. R. & JONES, D. A. (1984). Cross-sectional area and force production of the quadriceps. *Journal of Physiology* **353**, 53P.
- CURTIN, N. & DAVIES, R. E. (1973). Chemical and mechanical changes during stretching of activated frog skeletal muscle. *Cold Spring Harbor Symposium on Quantitative Biology* **37**, 619–626.
- EDWARDS, R. H. T., YOUNG, A., HOSKING, G. P. & JONES, D. A. (1977). Human skeletal muscle function: description of tests and normal values. *Clinical Science and Molecular Medicine* **52**, 283–290.
- GOLDBERG, A. L., ETLINGER, J. D., GOLDSPIK, D. F. & JABLECKI, C. (1975). Mechanism of work-induced hypertrophy of skeletal muscle. *Medicine and Science in Sports and Exercise* **7**(4), 248–261.
- GRINDROD, S., TOFTS, P. & EDWARDS, R. H. T. (1983). Investigation of human skeletal muscle structure and composition by X-ray computerised tomography. *European Journal of Clinical Investigation* **13**, 465–468.
- HÄKKINEN, K. & KOMI, P. V. (1985). Changes in electrical and mechanical behaviour of leg extensor muscles during heavy resistance strength training. *Scandinavian Journal of Sports Science* **7**(2), 55–64.
- HORBER, F. F., SCHEIDEGGER, J. T., GRÜNIG, B. E. & FREY, F. J. (1985). Thigh muscle mass and function in patients treated with glucocorticoids. *European Journal of Clinical Investigation* **15**(6), 302–307.
- IKAI, M. & FUKANAGA, T. (1970). A study on training effect on strength per unit cross-sectional area of muscle by means of ultrasonic measurement. *Internationale Zeitschrift für angewandte Physiologie Einschliesslich Arbeitsphysiologie* **28**, 173–180.
- JOHNSON, B. L. (1972). Eccentric versus concentric muscle training for strength development. *Medicine and Science in Sports and Exercise* **4**, 111–115.
- KATZ, B. (1939). The relation between force and speed in muscular contraction. *Journal of Physiology* **96**, 45–64.
- KOMI, P. V. & BUSKIRK, E. R. (1972). Effect of eccentric and concentric muscle conditioning on tension and electrical activity of human muscle. *Ergonomics* **15**(4), 417–434.
- LINDH, M. (1979). Increase of muscle strength from isometric quadriceps exercise at different knee angles. *Scandinavian Journal of Rehabilitation Medicine* **11**(1), 33–36.
- LOGAN, G. A. (1952). Comparative gains in strength resulting from eccentric and concentric muscular contractions. M.Sc. Thesis, University of Illinois.
- MCCULLOUGH, P., MAUGHAN, R. J., WATSON, J. S. & WEIR, J. (1984). Biomechanical analysis of the knee in relation to measured quadriceps strength and cross-sectional area in man. *Journal of Physiology* **346**, 60P.
- MCDONAGH, M. J. N. & DAVIES, C. T. M. (1984). Adaptive response of mammalian skeletal muscle to exercise with high loads. *European Journal of Applied Physiology* **52**, 139–155.
- MACDOUGALL, J. D., ELDER, G. C. B., SALE, D. G., MOROZ, J. R. & SUTTON, J. R. (1980). The effects of strength training and immobilization on human muscle fibres. *European Journal of Applied Physiology* **43**, 25–34.
- MACDOUGALL, J. D., SALE, D. G., ELDER, G. C. B. & SUTTON, J. R. (1982). Muscle ultrastructural characteristics of elite powerlifters and body-builders. *European Journal of Applied Physiology* **48**, 117–126.

- MORITANI, T. & DE VRIES, H. A. (1978). Reexamination of the relationship between surface IEMG and force of isometric contractions. *American Journal of Clinical Medicine* **57**, 263–277.
- RASCH, P. J. (1974). The present status of negative exercise – a review. *American Corrective Therapy Journal* **28** (3), 77–94.
- RUTHERFORD, O. M., GREIG, C. A., SARGEANT, A. J. & JONES, D. A. (1986). Strength training and power output – transference effects in the human quadriceps muscle. *Journal of Sports Science* **4**, 101–107.
- RUTHERFORD, O. M. & JONES, D. A. (1986). The role of learning and coordination in strength training. *European Journal of Applied Physiology* **55**, 100–105.
- RUTHERFORD, O. M., JONES, D. A. & NEWHAM, D. J. (1986). Clinical and experimental application of the twitch superimposition technique for the study of human muscle activation. *Journal of Neurology, Neurosurgery and Psychiatry* **49**, 1288–1291.
- SCHIAFFINO, S., BORNIOLI, S. P. & ALOISI, N. (1972). Cell proliferation in rat skeletal muscle during early stages of compensatory hypertrophy. *Virchows Archiv* **11**, 268–273.
- SELIGER, V., DOLEJAS, L., KARAS, V. & PACHLOPNIKOVA, I. (1968). Adaptation of trained athletes energy expenditure to repeated concentric and eccentric muscle contraction. *Internationale Zeitschrift für angewandte Physiologie Einschliesslich Arbeitsphysiologie* **26**, 227–234.
- TESCH, P. A. & LARSSON, L. (1982). Muscle hypertrophy in bodybuilders. *European Journal of Applied Physiology* **49**, 301–306.
- THORSTENSSON, A., HULTÉN, B., VON DÖBELN, W. & KARLSSON, J. (1976). Effect of strength training on enzyme activities and fibre characteristics in human skeletal muscle. *Acta physiologica scandinavica* **96**, 392–398.
- YOUNG, A. (1984). The relative isometric strength of Type 1 and Type 2 muscle fibres in the human quadriceps. *Clinical Physiology* **4**, 23–32.
- YOUNG, A., STOKES, M., ROUND, J. M. & EDWARDS, R. H. T. (1983). The effect of high resistance training on the strength and cross-sectional area of the human quadriceps. *European Journal of Applied Physiology* **13**, 411–417.